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BIOLOGY OF *HYADINA ALBOVENOSA* (DIPTERA: EPHYDRIDAE), A CONSUMER OF CYANOBACTERIA

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Abstract.—Information is presented on the life cycle and larval feeding habits of *Hyadina albovenosa* Coquillett, a common and widely distributed shorefly species of the subfamily Hyadininae and tribe Hyadinini. Larvae were found in nature only on soil-inhabiting colonies of *Anabaena,* a genus of Cyanobacteria (blue-green algae). Laboratory feeding tests indicated that the larvae can develop on a wide mixture of Cyanobacteria and even on such true algae as the diatom *Navicula pelliculosa* and the euglenophyte *Euglena gracilis.* Under laboratory conditions, the life cycle was completed in 18–19 days if *A. variabilis* served as the larval food. Eight generations a year can be produced in northeastern Ohio.

The larval food preference of *H. albovenosa* is contrasted and compared with those of other species of Hyadininae that utilize soil-inhabiting Cyanobacteria.

Key Words: Insecta, Diptera, Ephydridae, biology, *Hyadina albovenosa*

The superfamily Ephydroidea, consisting of 5 families (Curtonotidae, Camillidae, Drosophilidae, Diastatidae, Ephydridae), contains some 4000 species and has a worldwide distribution (McAlpine 1989). Undoubtedly the larger and better known families biologically are the Drosophilidae and Ephydridae whose larvae commonly have microphagous habits. Many species of Drosophilidae occur in forested habitats where they consume heterotrophic microorganisms, particularly yeasts (Ferrar 1987), whereas many species of Ephydridae occur in open, wetland habitats where their larvae feed on a wide variety of algae (Foote 1977, 1979).

Two of the more interesting assemblages of phycophagous Ephydridae are in the tribes Hyadinini (*Axysta, Hyadina, Lytogaster, Microlytogaster, Pelina, Pseudohyadina*) and Philygriini (*Nostima, Philygria*) of the subfamily Hyadininae (Mathis and Zatwarnicki 1990). Larvae of species of these two tribes seemingly are specialized for the consumption of Cyanobacteria (blue-green algae) (Foote 1977). The larval feeding habits of *Lytogaster excavata* (Sturtevant and Wheeler), *Nostima approximata* Sturtevant and Wheeler, and *Pelina truncatula* Loew have been elucidated in earlier papers (Foote 1981a, b, 1983).

This paper discusses the larval feeding habits of *Hyadina albovenosa* Coquillett and presents data on its utilization of different microbial species. Trophic resource partitioning among certain species of Hyadininae is also discussed.

Materials and Methods

All field work was carried out in northeastern Ohio in Portage County. The laboratory rearings and larval feeding tests were maintained in an environmental chamber programmed to give a photoperiod of 15L: 9D and a temperature of 22°C (+1°C). Most of the algae used in the feeding tests were obtained from the University of Texas Culture Collection of Algae (Starr 1978). Species lacking UTEX numbers in the list below were obtained from the Phycology Laboratory of Kent State University. Each algal species was cultured on nutrient agar in sterile Petri plates until a distinct algal lawn had appeared on the surface of the agar. Feeding tests were performed following the procedures given in Zack and Foote (1978). The algal monocultures used in the feeding tests are given below.

Cyanobacteria
  Anabaena flos-aquae (1444)
  Anabaena variabilis (B-377)
  Cylindrospermum sp. (LB-942)
  Gloeocapsa alpicola (B-589)
  Lyngbya spiralis (B-1831)
  Nostoc commune (584)
  Oscillatoria tenuis (B-428)
  Spirulina sp.
  Symploca muscorum (B-617)
  Synechococcus leopoliensis (625)
Euglenophyceae
  Euglena gracilis var. *bacillus* (L-884)
Chlorophyceae
  Chlamydomonas eugametos (9)
  Chlorella vulgaris (29)
  Cosmarium botrytis (175)
  Scenedesmus quadricauda (76)
Chrysophyceae
  Botrydiopsis alpina (295)
  Botrydium becherianum (158)
Bacillariophyceae
  Navicula pelliculosa (668)

LIFE HISTORY

According to Clausen (1983, 1984), the genus *Hyadina* in North America consists of 8 species. *Hyadina albovenosa* ranges from eastern Canada to Georgia and west to Arizona and on south to Mexico and El Salvador (Clausen 1983, fig. 31).

Deonier (1965) reported adults to be occasional inhabitants of the marsh-reed habitat. I found adults occasionally in sedge marshes, particularly in stands of *Carex stricta* Lam., but encountered them much more frequently in moist to wet mowed lawns. One particularly productive habitat consisted of an extensive grass lawn bordering a drainage ditch located near the Kent State University Field House. Other Ephydridae occurring at this site were *Hydrellia formosa* Loew, *Paracoenia fumosalis* (Fallén), *Scatella picea* (Walker), *S. stagnalis* (Fallén), *Leptopsilopa atrimana* (Loew), *Lytogaster excavata* (Sturtevant and Wheeler), *Philygria debilis* Loew, and *Nostima picta* (Fallén). The cyanobacterial genera *Anabaena, Cylindrospermum, Nostoc,* and *Oscillatoria* were abundant on the moist soil among the grass blades.

One female was reared from a third-instar larva feeding on a field-collected sample of *Anabaena* at the lawn site. The larva was collected on June 10, and the adult emerged on June 26.

Adults were particularly common at the lawn site during late spring and early summer, with the first seasonal record being May 4. Populations declined steadily as summer progressed, and the last seasonal record was obtained on August 15. A few adults were taken throughout June and July in weekly 20-sweep samples of nearly pure stands of *C. stricta* and reed canary grass, *Phalaris arundinacea* L., growing in a small marsh east of Kent.

Field-collected adults lived 10–35 days in laboratory cultures of *Anabaena variabilis,* but reared adults rarely survived more than 10 days on the same food substrate. Adults were relatively inactive but spent considerable periods of time feeding on the cultured lawn of *Anabaena*. Mating was observed within 3 days in a reared pair that had developed on *A. variabilis*. No overt courtship displays were noted, and it appeared that males attempted to mount any suitably sized individual, even those belonging to different ephydrid species. Copulation lasted 3–6 hours, and males continued to "ride" females after mating was completed in a manner similar to that described for *Nostima approximata* (Foote 1983). The single recorded pre-oviposition period, from emergence of the female to her first egg laying, lasted three days.

Females readily deposited eggs on cultured monocultures of a variety of blue-green algae, including species of *Anabaena, Calothrix, Cylindrospermum, Nostoc, Oscillatoria,* and *Spirulina.* However, females seemingly preferred *Anabaena* in mixed algal cultures. No or very few egg were deposited in cultures of other taxa of algae (greens, euglenophytes, diatoms, etc.), even if those non-cyanobacteria cultures were the only ones available to the females. A total of 453 eggs were deposited over an 18-day span by a field-collected female confined to a culture of *A. variabilis.* She began laying on May 30, the day after her capture, and continued to deposit 1–64 eggs daily until she died on June 15. Eggs were usually widely scattered over the surface of the algae. Each egg was covered with a thin layer of fecal material deposited by the female. Interestingly, the micropylar end of the egg never became overrun by algal filaments, suggesting that an antibiotic was present. In contrast, the remainder of the egg quickly became covered by a layer of algal trichomes. The incubation period of 10 eggs averaged 2 days (1.5–3.0 days).

Newly hatched larvae quickly began feeding on the algal lawn by pulling trichomes of *A. variabilis* into its oral cavity. This was accomplished through a raking action of the comb-like structures located on the facial mask on either side of and in front of the oral opening. Larvae fed gregariously on the algal lawn and displayed no obvious animosity to each other. They moved slowly over the algal surface and did not bury themselves into the substrate. As larvae moved across the algal lawn, they left behind an elongate track cleared of algae. Older larvae fed in a similar manner, and broken algal trichomes could be seen on the agar plate. The mouthparts moved relatively slowly and did not impart the flickering motion so typical of ephydrid larvae that are filter feeders of algal cells. Larval development (hatching to formation of puparium) was completed in an average of 5 days (n = 10). One day was spent in the first instar; 2, in the second, and 2, in the third instar.

A few hours prior to pupating, larvae ceased feeding, emptied the gut contents, and moved to a somewhat drier site on the agar substrate. Puparia commonly were clustered, with 2–5 puparia in each cluster. Both anterior and posterior spiracles usually projected above the algal lawn, whereas the central portion of the puparium frequently became covered with algae and detritus. The pupal period ranged from 8–9 days, averaging 8.5 days (n = 10).

Hyadina albovenosa is a multivoltine species in northeastern Ohio, requiring only 18–19 days to complete its life cycle (egg to egg) when reared on *A. variabilis.* This suggests that at least 8 generations a year could be produced in northeastern Ohio during a warm season extending from mid-May to mid-October.

Larvae completed development on 11 of the 19 tested algae, although the survivorship rate on different algae varied from 3 to 93 percent (Table 1). Nine of the 11 species of Cyanobacteria allowed for a complete life cycle. Only cultures of *G. alpicola* and *S. leopoliensis* were completely unsatisfactory. The most unexpected result was the relatively high survivorship (73%) of larvae reared on cultures of *Nostoc commune,* a taxon that was not used by *Lytogaster excavata, Nostima approximata,* or *Pelina truncatula* (Foote 1981a, b, 1983). Somewhat surprisingly, larvae also completed development on monocultures of the diatom *Navicula pelliculosa* and the euglenophyte *Euglena gracilis.* However, no record of the use of these two algae in nature was obtained.

There were strong differences in the larval and pupal periods of larvae developing on different species of algae (Table 2). The shortest combined developmental period (larval + pupal) occurred on *A. flos-aquae*

Table 1. Results of larval feeding tests for *H. albovenosa* using different algal monocultures.

Taxon	n	% Reaching Instar 2L	3L	P	A
Cyanobacteria					
Anabaena flos-aquae	30	100	97	87	40
Anabaena variabilis	30	100	100	100	93
Calothrix sp.	30	100	100	80	47
Cylindrospermum sp.	50	98	98	90	54
Gloeocapsa alpicola	20	0	—	—	—
Lyngbya spiralis	40	63	23	13	3
Nostoc communis	30	100	100	93	73
Oscillatoria tenuis	30	97	97	70	60
Spirulina sp.	30	100	93	83	73
Symploca muscorum	30	57	57	30	27
Synechococcus leopoliensis	30	100	50	33	0
Chlorophyceae					
Chlamydomonas eugametos	30	43	23	3	0
Chlorella vulgaris	20	25	0	—	—
Cosmarium botrytis	10	0	—	—	—
Scenedesmus quadricauda	10	10	0	—	—
Euglenophyceae					
Euglena gracilis	30	53	27	10	3
Bacillariophyceae					
Navicula pelliculosa	50	54	36	30	16
Chrysophyceae					
Botrydiopsis alpina	50	46	30	2	0
Botrydium becherianum	10	10	0	—	—

Table 2. Developmental period in days (larval plus pupal) of *H. albovenosa* feeding on eleven species of Cyanobacteria and algae.

Taxon	Developmental Period n	$\bar{x}$	s
Cyanobacteria			
A. flos-aquae	12	12.3	0.89
A. variabilis	28	14.1	1.24
Calothrix sp.	14	17.1	2.23
Cylindrospermum sp.	27	13.2	0.75
L. spiralis	1	17.0	1.73
N. commune	22	18.3	2.87
O. tenuis	18	13.6	1.09
Spirulina sp.	11	21.9	3.14
Symploca muscorum	8	17.4	1.19
Euglenophyceae			
E. gracilis	1	23.0	—
Bacillarophyceae			
N. pelliculosa	8	17.3	2.93

Table 3. Food preferences of newly hatched larvae of *H. albovenosa*. Each replicate consisted of five newly hatched larvae placed in the center of a ring of four algal plugs. Location of larvae after 24 h is given.

Alga	Replicate Number 1	2	3	4	5	$\bar{x}$
Test A						
A. flos-aquae	0	0	1	1	1	0.6
A. variabilis	3	5	4	2	4	3.2
Calothrix sp.	2	0	0	1	0	0.6
N. commune	0	0	0	0	0	0.0
Test B						
A. variabilis	3	5	4	2	2	3.2
Calothrix sp.	0	0	0	3	1	0.8
Cylindrospermum sp.	2	0	1	0	2	1.0
N. commune	0	0	0	0	0	0.0
Test C						
A. flos-aquae	2	0	0	0	0	0.4
A. variabilis	3	5	4	5	4	4.2
L. spiralis	0	0	0	0	0	0.0
O. tenuis	0	0	1	0	1	0.4
Test D						
A. variabilis	1	2	4	2	1	2.0
Calothrix sp.	1	3	1	0	2	1.4
L. spiralis	1	0	0	1	0	0.4
O. tenuis	1	0	0	2	2	1.0

(12.3 days); the longest, on *E. gracilis* (23.0 days). A long developmental period of 21.9 days was also obtained on the cyanobacterium *Spirulina* sp.

The results of the choice tests utilizing 4 sets of algal combinations (Table 3) showed that the larvae most commonly chose *A. variabilis*. Very few larvae chose *L. spiralis* and none selected *N. commune*. The order of preference was *A. variabilis* ≫ *Calothrix* sp. > *A. flos-aquae* = *O. tenuis* = *Cylindrospermum* sp. > *L. spiralis*.

DISCUSSION

Laboratory feeding results indicate that trophic resource partitioning occurs among

Table 4. Percent of four species of Hyadininae attaining adult stage on six species of Cyanobacteria in laboratory feeding tests.

Species of Cyanobacteria	Species of Hyadiniinae			
	Hyadina albovenosa	*Lytogaster excavata*	*Pelina truncatula*	*Nostima approximata*
A. flos-aquae	40	0	20	0
A. variabilis	93	70	100	20
C. sp.	54	40	100	0
L. spiralis	3	0	40	0
N. commune	73	0	0	0
O. tenuis	60	0	30	72

at least some of the four ephydrid species that utilize soil-inhabiting Cyanobacteria in northeastern Ohio (Table 4). *Nostima approximata* had a high survival rate on *O. tenuis,* a low rate on *A. variabilis*, and zero survival on six other species of blue-green algae. This species probably is a specialist on *Oscillatoria.* Unpublished data on *Philygria debilis* Loew, another member of the tribe Philygriini, indicate that it also is a specialist on *Oscillatoria. Hyadina albovenosa* was the only species that could develop on *Nostoc* and showed high survival rates on *Cylindrospermum* and *Oscillatoria* in the laboratory. Perhaps it should be considered as a generalist feeder of Cyanobacteria, although it was found only on *Anabaena* in nature. Little trophic segregation apparently occurs between *L. excavata* and *P. truncatula,* as both species had high survival rates on *A. variabilis* and *Cylindrospermum* sp. However, larvae of *P. truncatula* were able to complete development on *Lyngbya,* whereas those of *L. excavata* all died on this genus. None of the four species were able to utilize the unicellular genera *Gloeocapsa* and *Synechococcus.* In contrast, all four species produced adults from larvae feeding on the filamentous genera *Anabaena, Cylindrospermum,* and *Oscillatoria.*

Results obtained in laboratory feeding tests may not reflect actual use of Cyanobacteria in nature. Field collections of larvae actually feeding on different species of blue-green algae (Table 5) suggest that *H. albovenosa* is a consumer of *Anabaena, L. excavata* and *P. truncatula* prefer *Cylindrospermum,* and *N. approximata* and *P. debilis* utilize *Oscillatoria.* A single rearing of another species of Hyadinini, *Microlytogaster extera* (Cresson), suggests that larvae of that species utilize *Lyngyba* (Foote 1977).

Table 5. Utilization of soil-inhabiting Cyanobacteria by six species of Hyadininae in nature.

Hyadininae	Genus of Cyanobacteria			
	Anabaena	*Cylindropsermum*	*Lyngbya*	*Oscillatoria*
Hyadinini				
H. albovenosa	X			
L. excavata		X		
P. truncatula		X		
M. extera			X	
Philygriini				
N. approximata				X
P. debilis				X

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